



Review Paper

Adaptive marine conservation planning in the face of climate change: What can we learn from physiological, ecological and genetic studies?

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ABSTRACT

Rapid anthropogenic climate change is a major threat to ocean biodiversity, increasing the challenge for marine conservation. Strategic conservation planning, and more recently marine spatial planning (MSP) are among the most promising management tools to operationalize and enforce marine conservation. As yet, climate change is seldom incorporated into these plans, potentially curtailing the effectiveness of designated conservation areas under novel environmental conditions. Reliable assessment of current and future climate change threats requires the ability to map climate-driven eco-evolutionary changes and the identification of vulnerable and resistant populations. Here we explore the heretofore largely unrecognized value of information gained from physiological, ecological and evolutionary studies to MSP under ongoing climate change. For example, we explore how climate threats do not necessarily follow latitudinal gradients, such that both risk hotspots and refugia occur in mosaic distributions along species ranges – patterns that may be undetectable without knowledge of biological vulnerabilities at regional and local scales. Because co-occurring species can exhibit markedly different vulnerabilities to the same environmental changes, making ecological predictions requires, when possible, measuring the fundamental niches of key species (e.g., with the use of thermotolerance experiments). Forecasting also requires development of tools to identify the likelihood of community-level thresholds or tipping points (e.g., with the use of near-real world mesocosms), and assessment of the potential of populations for adaptation (e.g., with common garden experiments). Such research will facilitate better predictive models for the fate of populations, species, ecosystems and their functions. Ultimately, unfolding the complexity

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of the processes underlying climate change impacts will facilitate quantifying and reducing uncertainty in spatial planning decision processes and will enable the development of practical tools to validate adaptive conservation strategies.

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1. Introduction

Considering global and regional impacts of rapid climate change in conservation planning is a major societal challenge (Heller and Zavaleta, 2009; Pressey et al., 2007; Root and Schneider, 2006). Climate change is rapidly increasing in rate and magnitude (IPCC, 2013) and can alter the survival, fitness, phenologies and interactions of individuals, affecting population viability and food web dynamics (Doney et al., 2012; Poloczanska et al., 2013), which in turn alter the structure and functioning of ecosystems. While ultimately induced by anthropogenic warming, at the local scale, where conservation management is usually focused, these changes are proximately generated by comparably local scale conditions, both climatic and non-climatic in nature. This situation represents a fast-moving target under which protecting species, ecosystems and the services that they provide to human societies becomes a formidable task, requiring interdisciplinary science and many layers of information at multiple scales (Pressey et al., 2007). As on land, this undertaking is challenging in the marine environment, where current and future climate change impacts are, and will continue to be immense under almost any emission scenario (Gattuso et al., 2015). As an additional challenge, information on marine species distributions, ecology and evolution is often fragmented or non-existent, posing obstacles to ocean conservation management which are often greater than those in terrestrial systems (Carr et al., 2003; Richardson and Poloczanska, 2008).

The diverse impacts of climate change are almost certain to strengthen, and a key priority of ecological and conservation research is to understand how to better forecast the highly nonlinear effects of environmental change on ecosystems and the services they provide (Clark et al., 2001). These predictions are especially challenging given the novel, non-analogous environmental conditions presented by climate change (Fitzpatrick and Hargrove, 2009), which challenge assumptions of model stationarity and space-for-time substitution that are often used in modelling efforts (Refsgaard et al., 2014). In other words, we cannot always assume that patterns observed today are informative of future relationships. At the same time, conservation requires action, often even in the face of large uncertainty (Willcock et al., 2016). A decade ago, McLeod et al. (2009) highlighted the fact that climate change considerations are lacking in marine protected area (MPA) studies and proposed a list of general recommendations for best practices in MPA network design to build resilience to climate change, focusing primarily on coral reefs. More recently, Magris et al. (2014) reviewed 47 studies that considered climate change in marine planning (focusing mostly on the design and placement of MPAs) to examine how this topic is being addressed. The authors found that only 8.9% of the statements made were quantitative and ecologically justified. Of those, only 15% were derived from experiments incorporating climate change considerations. Magris et al. (2014) conclude that “strategies for considering connectivity and climate change in marine conservation planning must move towards explicit, quantitative objectives grounded in ecological knowledge”. However, in their review, Magris et al. (2014) did not detail in depth what this required ecological knowledge is.

To fill this gap and further advance marine conservation planning in the face of a rapidly changing climate, we draw upon the most recent concepts derived from the marine ecology, population genetics and physiology literature. We identify seven key interlinked scientific requirements where such information may be informative as a means of reducing or at least recognizing sources of uncertainty: (1) mapping shifts in species distributions; (2) understanding the physiological and ecological mechanisms behind climate-driven biological change; (3) identifying and predicting critical shifts in ecological states; (4) developing forecasting tools for communities and ecosystem functions; (5) assessing the adaptation capability of key populations and species; (6) developing tools and methods to address climate change in conservation prioritization; and (7) integrating information to develop adaptive conservation planning strategies for multi-stressor environments. Notably, our goal here is not to criticize current methods, but rather to highlight emerging approaches and to offer insights into methodologies that could be incorporated into future efforts, as well as to identify knowledge gaps that require further research.

2. Mapping shifts in species distributions

A quantitative understanding of the determinants of current and historical distributional range shifts of species is necessary to improve the prediction of future trajectories under different climate scenarios (Heller and Zavaleta, 2009). For example, our understanding of what factors set range edges can benefit from data charting previous shifts of leading and trailing range edges, which can in turn be matched against environmental data sets. However, distribution data are often not available, and insufficient or inadequate data can lead to artefacts in the detection of biogeographical range shifts (Bates et al., 2015). While climate is likely a critical determinant for most species distributions and range shifts, observed patterns are often the result of more complex processes reflecting the interaction and nonlinear dynamic of multiple environmental (e.g. weather, hydrographical conditions) and human –derived factors (e.g. pollution, habitat destruction). They also can reflect

the role of extreme events that occurred well in the past, disconnecting observed patterns from contemporary environmental conditions. For example, [Wetthey et al. \(2011\)](#) compared the observed distribution of barnacle species in Europe and found that their physiology should have allowed them to survive much further north than their observed distribution suggested. The current range boundary was likely set by an extreme winter in the 1960's, suggesting that the migrating distributional limit was recovering to its former extent and was not a response to climate change, *per se*.

Ocean warming is generally expected to lead to regional extinctions, and to poleward shifts of species ranges (tracking changing thermal conditions) associated with range contractions at the warm, tropical, edges ([Bates et al., 2014](#)) ([Fig. 1](#)). However, such shifts can be highly complex in both space and time, and include creeping expansions, range terminals, cul-de-sacs or even setbacks due to extreme cold events ([Burrows et al., 2014](#); [Canning-Clode and Carlton, 2017](#)). Species are not necessarily exposed to the most stressful environmental conditions only at the edges of their distribution, with hot-spots and cold-spots occurring within the entire range of their distribution ([Helmuth et al., 2002, 2006](#)). This implies that many species exist in geographic mosaics rather than more commonly-assumed latitudinal gradients ([Burrows et al., 2011, 2014](#); [Kuo and Sanford, 2009](#)), with some range limits also being set by lack of suitable habitat occurring within the thermal ranges of species ([Mieszkowska et al., 2006](#)). Thus, not all impacts of climate change will occur only at poleward and equatorial range edges. Although the potential importance of such spatial heterogeneity is often acknowledged, it is largely ignored when parametrizing analytical tools for projecting species ranges, such as climate envelope models ([Hijmans and Grahams, 2006](#); [Pearson et al., 2009](#)). They are, however, detectable using more mechanistic approaches that consider physiological vulnerability ([Woodin et al., 2013](#)).

Recent studies show species-specific responses to climate change, with range shifts occurring at different rates across marine taxa and in different regions ([Lima et al., 2007](#); [Mieszkowska et al., 2006](#); [Pinsky et al., 2013](#)). For example, the leading range edge of the Lusitanian trochid *Phorcus lineatus* (da Costa) has extended by 10 km per decade since the 1980s, whereas the range extension of the Lusitanian barnacle *Chthamalus montagui* (Southward) is a factor of ten less across the same period along the UK coastline ([Mieszkowska et al., 2006, 2014](#)). It is therefore important to compile information at spatial and temporal scales relevant to the life history of each species, and probe the processes by which alternative factors affect the dynamics of populations ([Almpanidou et al., 2016](#)). At the center of this research are sustained observations of the abundance and distribution of key marine species, even highly mobile ones (e.g., sea turtles, [Mazaris et al., 2017](#)). Moreover, not all impacts of climate change are detectable as lethal events that result in range shifts. Range edges can be characterized by increased genetic isolation, genetic differentiation, and variability in individual and population performance, but conclusive evidence is often lacking ([Sexton et al., 2009](#)). Understanding the extent to which such variation occurs is critical because it can determine population-level vulnerability to future events, and populations with low genetic variance can appear healthy under contemporary conditions but may be highly susceptible to even slight changes in environmental conditions. It is also critical to consider multiple life history stages. For example, in sea turtles, nest temperature determines hatchling sex ratios, which raises concerns about an uncertain future for some populations ([Poloczanska et al., 2009](#)). Still, even for populations with extreme female-biased hatchling sex ratios, a balanced adult sex ratio on the breeding grounds could be sufficient to ensure long term viability ([Poloczanska et al., 2009](#)). Clearly, significant range shifts of ecologically and/or economically key species present a challenge for conservation planning as it is difficult to protect a species in a specific area of jurisdiction

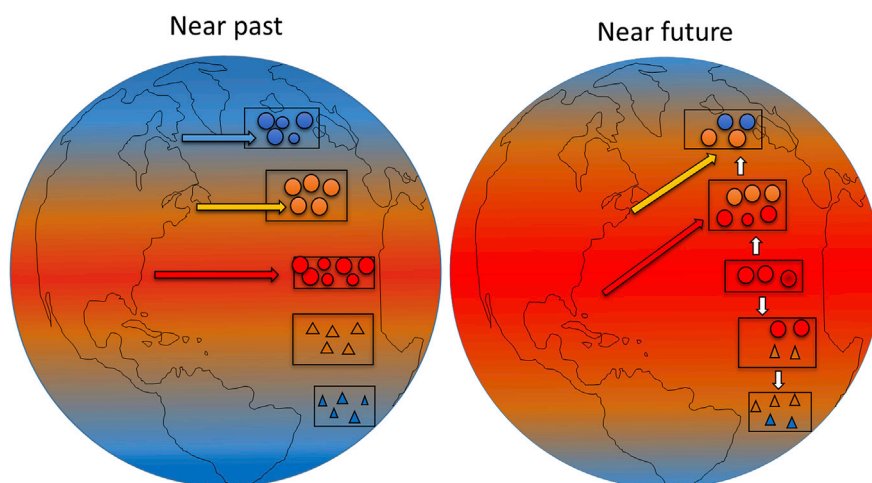


Fig. 1. Illustration of possible impacts of climate change on species distributions from the near past to the near future. Sensitive tropical (red symbols) and boreal (blue symbols) species are expected to go locally or globally extinct while other tropical as well as temperate species expand (white arrows) poleward. Adaptation through selection or fast evolution to more resistant genotypes is also possible. Bioinvasions (coloured arrows) that in the past might move mostly horizontally across the same latitudinal zone, can, under global warming, cross, for example, from tropical to warming temperate regions. (For interpretation of the references to colour in this figure legend, the reader is referred to the Web version of this article.)

where it is disappearing because conditions are getting too hot there (e.g., Hill et al., 2015). As such, plans need to be adjusted when such species disappear in some areas and move into new territories.

Unsurprisingly, long-term monitoring programs producing extensive time series for marine species are primarily present in nations with stronger economies (see Appendix in Supplementary Information for examples). These programs still face challenges related to data access, data sharing, availability of historical data, and continuity of time-series across socio-political borders. And, even in cases where reasonable time series exist, we still lack much basic scientific information related to physiological vulnerability of key species, and the genetic underpinnings of that vulnerability (Kelly, 2019). We explore many of these ideas in the next section.

3. Understanding the physiological and ecological mechanisms behind climate-driven biological change

Although the description of biogeographic shifts is highly valuable in the context of climate change, understanding the biological mechanisms (e.g., assessing the fundamental and realized niche spaces of key species) behind those changes can offer critical insights for conservation planning (e.g., Thuiller et al., 2005). It is especially critical for understanding the likely impacts of non-analog suites of environmental conditions expected under climate change, which suggest that simple correlations with historical and observed shifts in range boundaries may be insufficient for forecasting future ecological impacts. If conservation planning is only based on climate history and its relation to range boundaries, then there is a severe risk of failure (Woodin et al., 2013). Here, a wealth of information at physiological, ecological and evolutionary scales can again provide valuable insights. We discuss in this section advances and gaps in knowledge in four topical areas that are critical for a mechanistic understanding of climate change impacts in the marine realm. The first two address mechanisms at individual, population and species levels (physiological vulnerability) and at the level of communities to ecosystems, while the last two address how temporal and spatial variability at a range of scales may create refugia and affect different levels of organization.

3.1. Impacts at the individual, population and species levels (physiological vulnerability)

The recent surge of investigations on shifting species distributions as a consequence of successful invasion or in response to shifting environmental conditions (e.g., tropicalization, Vergés et al., 2014) has re-focused attention on physiological tolerance (e.g., Gunderson and Stillman, 2015; Martínez et al., 2015). Physiological sensitivity varies among drivers (e.g. heat wave, hypoxia, ocean acidification) and species (Harley et al., 2017) and co-occurring drivers interact to buffer or enhance each other (e.g., Wahl et al., 2011), leading to both antagonistic and synergistic effects (Crain et al., 2008). The constituents of a multifactorial regime may shift independently of each other in time and space (e.g., Gunderson et al., 2016). Moreover, vulnerability can vary considerably among populations of the same species due to evolutionary processes (e.g. local adaptation or genetic drift, Crisci et al., 2017), so that vulnerability at one site can be distinct from that of populations at other portions of that same species' range (Kuo and Sanford, 2009). Inter-individual responses can even vary significantly within the same population, complicating species-level predictions (Dong et al., 2017; Kuo and Sanford, 2009). For example, Dong et al. (2017) showed that variability in heat tolerance among individuals within populations of three species of snails in China exceeded variation among the species.

Any persistent mismatch between the physiological comfort zone and important environmental parameters will decrease individuals' performance (e.g., Pörtner, 2001). Accordingly, individual fitness and competitive abilities can differ among seasons or between populations located at the core and the edge of a distributional range (e.g., Araújo et al., 2014); and the impact of changing climate is also expected to vary accordingly. For instance, populations close to trailing range limits are expected to be subjected to increasing thermal stress from warming (Mota et al., 2015), whereas populations near leading edges are assumed to benefit from amelioration of cold thermal regimes (Harley et al., 2017; Helmuth et al., 2002). However, when drivers display mosaic patterns along a latitudinal range, especially in extreme environments like the rocky intertidal zone (Helmuth et al., 2006; Kroeker et al., 2016), variation in physiological stress impacts will also occur at these finer spatial scales (Kuo and Sanford, 2009; Place et al., 2008). For instance, in the above example (Dong et al., 2017) levels of stress were as high in some center populations as they were at edges due to the influence of local environmental factors. Understanding the spatial and temporal scales over which environmental stress affects individuals' performance is thus critical to scale-specific mitigation and/or adaptation measures of the direct and indirect impacts of climate change (Bates et al., 2018; Kelly, 2019).

3.2. Impacts at the ecosystem level

Changes in factors such as temperature and pH that are stressful to one species may simultaneously improve performance in another (Harley et al., 2017), and the direction of impacts may vary seasonally (e.g. Graiff et al., 2015b). When two species are transiently impacted with unequal severity, their interaction(s) (i.e., predation, competition, symbiosis, parasitism, infection) can shift in strength or could even reverse (Kordas et al., 2011). Whenever these interactions are strong, their shift has the capacity to modulate the effects of the driver on one or both of the interacting species (Connell et al., 2017). When direct (physiological) and indirect (ecological) stress leads to a change in the abundance of individuals of a key species, communities re-structure. Nonetheless, not all ecosystems are equally vulnerable to global change (Halpern et al., 2007), and not all species replacements lead to a change in ecosystem functions and services. Many do (Doney et al., 2011) however, as

particularly apparent in arctic systems (Wassmann et al., 2011), coral reefs (Hoegh-Guldberg and Bruno, 2010) and seagrass habitats (Nyström et al., 2012).

Under ongoing environmental change, communities reorganize in ways that are not always predictable from individual species' responses. When some species respond to ocean warming with a phenological shift (e.g. change in the onset of life cycle events, such as reproduction or migration), trophic interactions may be disrupted, with far greater consequences for community functioning than the direct, physiological impact of higher temperature might suggest (Aberle et al., 2012; Edwards and Richardson, 2004; Thackeray et al., 2010). Similarly, different rates of spatial shifts in response to warming can provoke profound community re-structuring (e.g., in plankton, Chivers et al., 2017), and so can shifts from native to alien species (Byrnes et al., 2007), with possible severe consequences to community dynamics and ecosystem functions.

Profound community restructuring may lead to a loss of ecosystem functioning and services which can alter the intended effectiveness of protected areas (Bellwood et al., 2003). Alternatively, when native species are extirpated due to climate change but are replaced by functionally-equivalent, non-indigenous and more resistant species, theoretically little or no loss of ecosystem functions and services is expected (Quijón et al., 2017). Understanding the underlying mechanisms that result in modifications and reconstruction of communities will improve our understanding of the impacts of climate change on ecosystem services (Scholes, 2016). To achieve this, information on species traits (Bremner et al., 2006; Estrada et al., 2016; Sunday et al., 2015) and reliable measurements of ecosystem functions (which entails elaborate field or lab experiments, see section 5 below) over appropriate temporal and spatial scales, are required.

3.3. Contrasting roles of environmental variability

To make realistic predictions about the fate of species and ecosystems in the wake of global change, we need to consider not only changes in average conditions but also the frequency, intensity and sequence of environmental fluctuations (Helmuth et al., 2014; Wahl et al., 2013). Several recent studies have pointed to the long-lasting impacts of rare but extreme events in setting distribution limits (Wetthey et al., 2011) and in reducing the genetic diversity of populations (Pearson et al., 2009). Specifically, fluctuations that expose organisms to short-term yet lethal extremes can be far more important to species distributions than changes in mean conditions (Helmuth et al., 2014; Wetthey et al., 2011). Due to the nonlinear nature by which factors such as temperature affect performance and survival, even modest deviations from mean conditions can have significant implications for our ability to predict biological response (Woodin et al., 2013). Conversely, environmental fluctuations can also modulate or ameliorate stressful mean conditions (Benedetti-Cecchi et al., 2015). Fluctuations around a moderately stressful mean (e.g. hypoxia) may represent alternating phases of high stress (e.g., anoxia) with partial mortality, and low stress (e.g., normoxia) with the potential for recovery, growth and reproduction. Fluctuations thus may mitigate the net impact of a given stressor and promote adaptation to novel environmental conditions (Fig. 2).

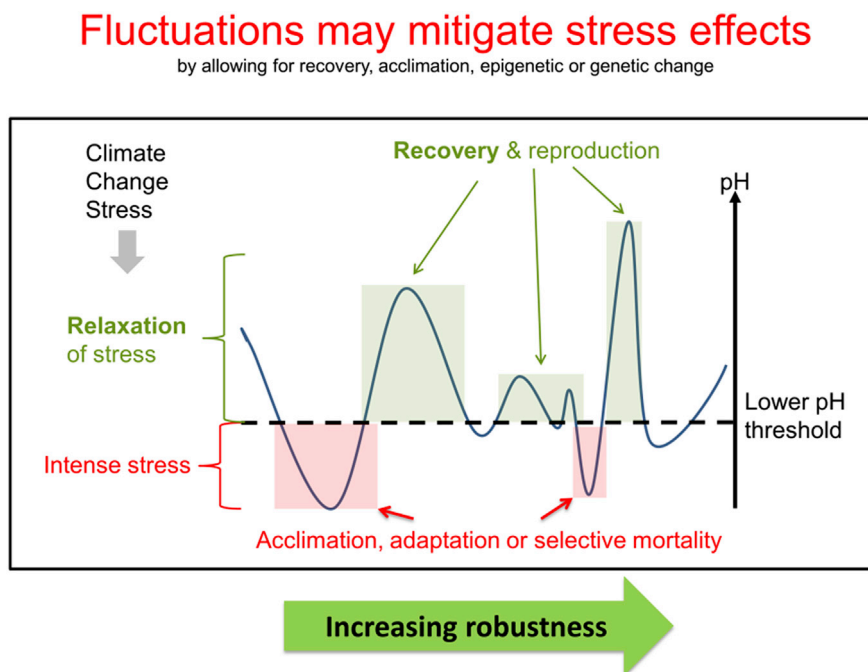


Fig. 2. Illustration of different kind of fluctuations with different magnitude, duration, frequency and direction. Here illustrated for pH, these fluctuations can represent exposure to extreme detrimental conditions or conditions potentially leading to recovery. Over time, exposure to fluctuations can facilitate phenotypic plasticity, selection for more adapted genotypes, or other mechanisms increasing the robustness of the population. Modified after Wahl et al. (2015).

Despite widespread recognition of the importance of temporal environmental variation, studies of the effects of climate change-induced variations in temperature on marine communities remain relatively rare (reviewed by [Thompson et al., 2013](#)). Results of controlled experiments conducted under more realistic environmental variability (e.g., incremental warming or acidification that also follow daily natural fluctuations, [Wahl et al., 2015](#)) have begun to offer insights, such as the differential effect of ocean warming and acidification in different seasons and their effects on defence mechanisms of seaweeds (e.g., [Graiff et al., 2015a](#); [Raddatz et al., 2017](#); [Werner et al., 2016](#)). The biological response to environmental variability will depend on several metrics describing the fluctuations: the distance of the mean from an organism's optimum, the duration, amplitude and frequency of the fluctuation, and the means and fluctuations of other environmental factors (e.g., [Wahl et al., 2016](#)). A gentle slope of seasonal warming permits acclimation, whereas the steep slope of a heat wave may not. The sequence of fluctuations of different factors ([Kroeker et al., 2016](#); [Williams et al., 2011](#)) and the amount of temporal overlap may determine the degree to which multiple stressors are synergistic or antagonistic in their interaction ([Gunderson et al., 2016](#)).

3.4. Stepping stones and refugia

Small-scale spatial and temporal heterogeneity in environmental factors (e.g. temperature, pH, oxygen) may offer refugia from stress ([Hannah et al., 2014](#)). This has been described in physically or biologically structured habitats such as rocky shores (e.g., [Lima et al., 2016](#)) or kelp forests (e.g., [Hurd, 2015](#)). Spatio-temporal variability in conditions may be enhanced by local nonclimatic stressors ([Harley et al., 2006](#)). For instance, abiotic parameters (e.g., sea surface temperature, pH) do not necessarily operate along gradients, and, as mentioned above, can display mosaic patterns driven by local conditions (shoreline orientation, slope, currents etc.). One recent large-scale study showed that areas of highest physiological stress and greatest risk of ecosystem collapse occur at sites where multiple stressors coincide in space and time ([Kroeker et al., 2016](#)). The ability to prioritize 'future habitats' through identification of holdouts, stepping stones and small-scale refugia, is increasingly acknowledged as an alternative conservation strategy ([Hannah et al., 2014](#); [Jones et al., 2016](#); [Queirós et al., 2016](#)). Hybrid models and knowledge of species physiological tolerance limits and vulnerability (the fundamental niche) as well detailed mapping of the environment at multiple scales are crucial in the application of such a strategy ([Petchey et al., 2015](#)). Realistically, this cannot be done for every species, but applying these approaches for ecologically and economically important species ([Woodin et al., 2013](#)) will generate more accurate predictions and improve our ability to manage marine ecosystems.

4. Identifying and predicting critical shifts in ecological states

How do the many confounding factors and complexities described above affect our ability to produce forecasts that have actionable implications for policy and management ([Petchey et al., 2015](#))? Generalizations such as poleward range shifts and general declines in physiologically vulnerable species, while made with more confidence when considered over long time scales (decades to centuries), are often less useful for enacting policy at local or regional levels ([Mangano et al., 2019](#)). Nevertheless, there are opportunities for applying our understanding of the biological impacts of environmental change on marine ecosystems to scales that are relevant to policy and management ([Selkoe et al., 2015](#)).

4.1. Early warning systems

Climate change leads to "winners and losers", where some species respond positively (i.e. increased fitness) to environmental change, whilst others in the same assemblage exhibit negative responses ([Somero, 2010](#)). An important, but often overlooked consideration is that organisms ultimately respond to patterns in weather, which are transient but are eventually driven by large-scale, long-term shifts in climate ([Helmuth et al., 2014](#); [Stenseth et al., 2002](#)). For example, a warm summer in 2012 in the Gulf of Maine had significant impacts on the growth rates of American lobster, which in turn had enormous socioeconomic impacts on regional fisheries ([Mills et al., 2013](#)). Several researchers have suggested the creation of *early warning systems* based on indicators (reviewed in [Gregg et al., 2011](#); [Kershner et al., 2011](#)) whereby vulnerability of populations is estimated based on short-term forecasts (months-years) coupled with knowledge of physiological vulnerability. The summer of 2012, for example, witnessed temperatures in the Gulf of Maine that were 3 °C higher than the climatology ([Pershing et al., 2015](#)), leading to significant negative impacts on lobster populations ([Mills et al., 2013](#)). As [Mills et al. \(2013\)](#) describe, these biological responses were predictable based on a scientific understanding of lobster biology even early in the season as anomalously warm temperatures continued to rise, yet no policy in either the U.S. or Canada, for example modification of catch limits, existed to contend with the impending impacts. Flexible policies that enable rapid responses to predictable, near-horizon changes, for example by switching target species ([Pinsky and Fogarty, 2012](#)), will become increasing critical yet are still in their infancy in many if not most parts of the world ([Gregg et al., 2011](#)).

4.2. Tipping points and extreme events

The gradual increase in multifactorial environmental pressure, especially when superimposed by single or repeated extreme events, may push a community beyond a tipping point (i.e. an ecological threshold) leading to fundamental

structural and functional ecosystem alterations (phase or regime shifts) (Lubchenco and Petes, 2010). Since, theoretically, the return to the original state is often lengthy or impossible (Reyer et al., 2015; Scheffer et al., 2009), and commonly requires a greater environmental change than the one that caused the shift, it is crucial to identify signals of an impending tipping point (Lenton, 2013). The ability to identify tipping points could aid management decisions or proactive plans for adaptation (Horan et al., 2011).

Although some extreme events can be catastrophic, the recurrence of sub-lethal extreme events might also serve as a “selection pump” for more resistant phenotypes (through physiological or behavioural plasticity, epigenetic mechanisms and/or adaptation) and may thereby enhance fast evolutionary processes (Ketola and Saarinen, 2015; Pansch et al., 2014). The ultimate result of extreme events will depend on the background stress level, the nature and the recurrence of the event. The combination of background (chronic) and pulse stress(es) may overcome natural mechanisms of resilience such as wide tolerance margins, phenotypic plasticity or high genetic diversity. When the background level is benign (no other stressors), the “resilience hill” preventing the shift should be high, but under persistent stress of other pressures the hill for a new stress will erode (the tipping point will be lower) and therefore the shift would be easier (Fig. 3).

Despite the potentially severe consequences of phase shifts in response to extreme events, we know little about how environmental variability may provoke ecological tipping under realistic conditions (Kreyling et al., 2014; Thompson et al., 2013). Despite the range of approaches and statistical methods, identifying ecological thresholds and regime shifts in ecological time series can be a challenge (Andersen et al., 2009; Johnson, 2013). In tightly-controlled experimental settings, this may be achievable at much shorter time scales with the development of well-defined and measurable signals for such shifts based on process-level understanding (e.g., Mangano et al., 2019). Recent intertidal field experiments indicate that such early warning indicators for regime shifts can be detected (Benedetti-Cecchi et al., 2015; Rindi et al., 2017), but much more research is needed in this area.

5. Forecasting tools for communities and ecosystem functions under climate change impacts

As mentioned above, many complexities challenge forecasts of ecological responses to climate change at scales relevant to management, especially over longer time horizons (Petchey et al., 2015). An increasingly sophisticated toolset of models and experimental approaches is attempting to merge generalizability over large scales with details on local environmental change, population characteristics and species traits to make usable forecasts (reviewed in Kish et al., 2016; Olsen et al., 2016; Torossian et al., 2016). Investigations of climate velocity, for example, allow an exploration of the regional rates of change in parameters such as water temperature, which can be coupled with the capacity of populations to physiologically, behaviourally or even evolutionarily respond to those signals (Burrows et al., 2014; Pinsky et al., 2013; Sunday et al., 2015).

A new breed of “hybrid” models has incorporated the strengths of both correlative and mechanistic approaches through a series of multi-step models where the results of one model type overlay those of the other (Briscoe et al., 2016; Pacifici et al., 2015). These methods allow for quantification of uncertainty in model outputs, which can vary among species and among geographic locations (Wenger et al., 2013). To date, however, most models have focused on terrestrial organisms, and there is a dearth of comparable studies in marine systems (Torossian et al., 2016). An increasingly important approach for developing mechanistic understanding of the impacts of climate change on marine communities is the use of mesocosm experiments which open windows into the future of communities through manipulative experiments in near-natural conditions. Such innovative near real-world mesocosm systems have been used to great effect in recent years. One example is GEOMARS

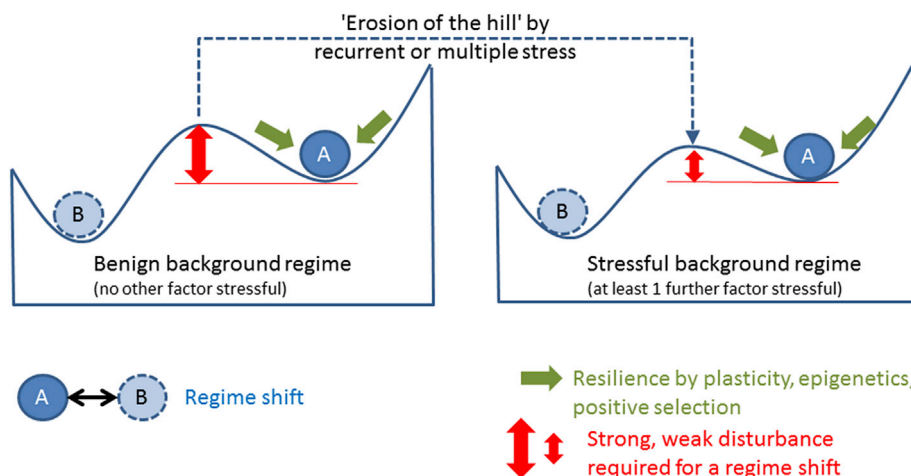


Fig. 3. Weaker or fewer extreme events (erosion of the ‘hill’ separating two phases A and B) are needed to trigger a phase shift when background stress is high (right panel) than when background stress is low (left panel).

benthic mesocosm system in Kiel (Germany) that uses computer-controlled flow-through delta treatments that follow natural fluctuations to simulate both warming and acidification conditions, separately and in combination (Wahl et al., 2015) (see Appendix in Supplementary Information). Extrapolating results from mesocosms to spatial management scales is the next important step.

6. Assessing the capacity for adaptation to novel environmental conditions

Genetic diversity can play a crucial role in driving complex distribution patterns, and determine how populations will respond to the changing climate in a particular location (Kelly, 2019). Accordingly, maintaining large population size to support high genetic diversity is widely acknowledged as a fundamental step in conservation biology (e.g., Hedrick, 2001), but more recent studies have also pointed to the role of environmental heterogeneity (Kelly, 2019). Edge (marginal) populations can be less genetically diverse and thus more sensitive to environmental change, but on the other hand they may encompass unique local adaptations (as was shown in an Asian mangrove study, Arnaud-Haond et al., 2006), that may better handle future climates and thus should be of particular interest for conservation strategies. This research focus is not well developed yet, but there is a marine example showing that the low genetic diversity of populations of an intertidal macroalga at the extreme (“frayed”) edges of its distribution were important in determining population stability (Pearson et al., 2009). This suggests that levels of inter-individual vulnerability within populations may play a key role in determining how range edges will respond or adapt to environmental change.

Reliable predictions of the responses of populations of ecologically and economically important species in the face of novel and rapidly evolving environmental conditions are a key for conservation planning. At the microevolutionary scale, phenotypic plasticity and contemporary (rapid) evolution may reduce the risk of local and global extinctions (Calosi et al., 2016; Reusch and Wood, 2007). Two different types of plastic responses are possible: the classical adaptive phenotypic plasticity (i.e. production of different and advantageous phenotypes by the same genotypes in response to a change in the environment, Via et al., 1995), and the phenotypic buffering (i.e. the maintenance of a functional phenotype by a genotype facing an environmental stress, Bradshaw, 1965). While distribution shifts and phenotypic plasticity will temper the negative impact of climate change, adaptation remains the ultimate response of a population to environmental change (Calosi et al., 2016).

The realization that on-going environmental changes can drive rapid selection in natural populations within only a few generations (Hendry and Kinnison, 1999; Reznick and Ghalambor, 2001) supports the idea that contemporary evolution will play an important role in the current biodiversity crisis, and should play a role in marine conservation planning. Nevertheless, while the potential for phenotypic plasticity and contemporary evolution has been addressed by a flourishing literature (see Reusch, 2014), the actual responses reported from natural populations are often far from the expectations, and thus remain particularly challenging to predict (Crozier and Hutchings, 2014). This discrepancy between predictions and field observations is a consequence of our fragmented comprehension of the complex interactions between natural populations and their local environment (Kelly, 2019). Characterizing the interaction between the eco-evolutionary processes and environmental factors driving phenotypic divergence in natural populations is a critical step needed to improve our predictive capacity on populations' responses to climate change (Almpanidou et al., 2017).

Local adaptation (i.e. the divergent selection leading to locally adapted individuals exhibiting higher fitness in their habitat than foreign individuals, Kawecki and Ebert, 2004) and phenotypic plasticity may promote or hamper the evolution of populations facing climate change (Ghalambor et al., 2015). The combination of experimental ecology and next-generation –omics technologies (including genomics, epigenomics, transcriptomics and metabolomics) represent an unprecedented opportunity to characterize the patterns of local adaptation and phenotypic plasticity in natural systems and, ultimately, to understand the complex relationships between phenotype, genotype and environment in the context of climate change (de Villemereuil et al., 2016; Stillman and Armstrong, 2015).

One useful tool to test for local adaptation is common garden experiments, where individuals from different origins are submitted to a common biotic (e.g. high predation) or abiotic (e.g. high temperature) environmental factor, and their responses are compared. Common garden experiments can be conducted *in-situ* (e.g., Ledoux et al., 2015) or in controlled conditions (e.g., Arizmendi-Mejía et al., 2015). Integrating genomics, epigenomics, transcriptomics and metabolomics to these experiments allows comparing genetic polymorphisms, epigenetic variations, levels of gene expression or protein concentrations between treatments, between different ecotypes or morphs, at different times of sampling or developmental stage, or along a natural environmental gradient (e.g. depth). Different levels of molecular organization can thus be considered (i.e. from a single gene to groups of genes based on their metabolic function, including entire biosynthesis pathways or gene families) and compared to the phenotypic responses allowing an accurate understanding of the underlying eco-evolutionary processes. The number of studies involving experimental and –omics approaches to decipher population-by-environment interactions is increasing sharply (e.g., Palumbi et al., 2014; Pespeni et al., 2013) and this should significantly improve on our ability to design relevant conservation plans.

Genetic enhancement of marine species to increase their tolerance to climate change has been recently emphasized as a potential tool to improve conservation outcomes (e.g., van Oppen et al., 2015). This assisted evolution involves different options such as assisted gene flow, epigenetic programming or selective breeding, and was mainly proposed for the restoration of coral reefs (Van Oppen et al., 2017). While promising, its efficiency may vary among species depending on life history

traits (e.g. generation time). Moreover, its feasibility over geographic scales relevant for conservation planning remains to be evaluated, and the ethics of this approach is also still debatable.

7. Current and emerging tools and methods to address climate change in conservation prioritization

Various approaches and risk-management tools have been developed and applied to enable policy makers and environmental managers to efficiently prioritize conservation areas and the allocation of efforts across space (e.g., Ando and Mallory, 2012; Carvalho et al., 2011; Jones et al., 2016; Shah et al., 2017). According to a recent review (Jones et al., 2016), the most common approach in the face of climate change is the use of niche/bioclimatic modelling or species distribution models (SDMs) to forecast future species distributions, and consequently the use of a spatial prioritization software such as Marxan (Ball et al., 2009) or Zonation (Moilanen, 2007) to select conservation priority sites based on the forecasted distributions.

The limitations of the use of correlative SDMs, which assume space for time substitution, has been widely discussed as well as the need to add mechanistic information to improve them (Beaumont et al., 2005; Heikkinen et al., 2006). Several methods and tools to deal with uncertainty in species distributions have been developed, for example by including dynamic subsurface variables into the modelling processes (Brodie et al., 2018), by incorporating eco-physiological responses derived by experimental work (Franco et al., 2018), such as combining experimental thermal performance data of species into correlative SDMs (Talluto et al., 2016). An expanding number of studies from the marine environment have included such approaches into energetic models which are then used to generate spatially-explicit predictions not only of species distributions but also of growth and reproduction (e.g., Mangano et al., 2019; Montalto et al., 2016; Thomas and Bacher, 2018). Nevertheless, there is a need for improved tools that account for the underlying mechanisms of shifts in ecological states and the adaptation capabilities of species (see previous sections).

The establishment of networks of MPAs is often listed high in scientific agendas as an effective tool to mitigate the impacts of climate change at regional scales (Mason et al., 2017; Roberts et al., 2017). Systematic conservation planning could indeed offer a solid basis for enhancing conservation. The identification and inclusion of refugia habitats (i.e. areas less affected by climate change) in conservation plans is a promising approach to help mitigate for climate change implications (Jones et al., 2016; Keppel et al., 2015), especially when these refugia are assembled as a well-connected network or series of “stepping stones” (Hannah et al., 2014). Strategies include using climate forecasts and prioritizing areas where climate change will not have considerable effect (Levy and Ban, 2013), identifying where current and future distributions overlap (Terribile et al., 2012), or using historical or current climatic factors (Hermoso et al., 2013). Another prioritization goal can be to increase spatial heterogeneity for conservation by selecting areas with diverse abiotic or bioclimatic characteristics, supporting a variety of future ecological systems and processes and thus increasing the resilience of the entire network (Jones et al., 2016). Such an approach does not rely on uncertain climatic and species distribution forecasts and costly data, and will most probably be most effective when it also incorporates biological data such as those suggested in the previous sections. At the same time, it should not be biased towards regions or sites (e.g. coastal, neritic) where more information is available and should offer spatially explicit recommendations for directing protection schemes at habitats and sites which are often underrepresented (e.g. deep sea). A recent example for the North Sea used a novel approach based on spatial meta-analysis of climate impact models to improve the positioning of MPAs to limit climate change and ocean acidification impacts (Queirós et al., 2016).

Increasing connectivity in a network of protected areas so that species can track suitable habitats as weather and climate change has also been proposed as an approach to address climate change (Gaines et al., 2010). However, it is difficult to accommodate the differing requirements of multiple species. By contrast, Hodgson et al. (2009) argued that the importance of connectivity has been overemphasized and that investing in other strategies such as maintaining and increasing the area of high quality habitats, prioritizing areas of high environmental heterogeneity, and controlling human pressures might be more beneficial. These contrasting views emphasize that further work on this topic is needed. As mentioned in our Introduction, Magris et al. (2014) found that very few studies on MPAs and connectivity currently use actual ecological data to make decisions, demonstrating that we still have a long way to go to achieve this.

8. Adaptive conservation planning strategies under climate change

Conservation planning that ignores potential climate change impacts or that is based on unrealistic generalizations, will result in conservation targets or indicators that are unlikely to be achieved. Even if all the physiological, ecological and evolutionary knowledge listed above would be available, several factors could still hamper a sound scientific advice on climate adaptation in decision-making processes. In light of these challenges, below are some suggested approaches and possible solutions for dealing with this complex issue.

As ecological communities continue to be reshuffled, new interactions will arise with unpredictable ecological results. Thus, key species may disappear from a region but other species (range-expanding or alien), could replace ecological functions or support economic viabilities (see Appendix). Marine conservation strategies should have clear and operational objectives (Katsanevakis et al., 2011), which in view of climate change, especially in some land-locked seas as the Mediterranean, *might need to shift from a species-based to an ecological functions approach* (Mačić et al., 2018). A clear conservation end goal is

thus needed, whether it is maximum extraction, preserved ecosystem functions, preserved local biodiversity or just high biodiversity, regardless of origin.

Improving our ability to predict the interactions of climate change with local human-induced pressures such as habitat destruction, pollution or selective extraction is urgently needed (Crain et al., 2008). One mechanism to transfer knowledge on the combined effects of human activities and natural processes on the environment into policy are cumulative effect assessments (CEAs) since they offer holistic evaluations within the science-policy interface (Stelzenmüller et al., 2018). Representing a specific form of environmental impact assessments, CEAs investigate the cause-effect pathways of various human activities and ecosystem components, exploring the risk of altering ecosystem state and functions through a combination of human pressures. Hence, *embracing an integrated and structured CEA as part of an adaptive conservation planning process would enable a systematic consideration of climate change.*

The next step beyond the recognition and consideration of climate change in conservation prioritization is the actual implementation of adaptation or mitigation strategies by the means of an ecosystem-based management (EBM). *EBM is seen as a way forward to integrate marine conservation with the spatial management of human activities* (Katsanevakis et al., 2011; Selkoe et al., 2015). EBM is an adaptive management process that accommodates, through the elements of monitoring and evaluation, adjustments to changing conditions or unforeseen ecosystem responses. This puts a spotlight on the fact that the science-policy interface is shaped as an interactive process (Petes et al., 2014), so that relevant and more targeted information and predictions on species and community shifts, eco-evolutionary changes, risk hotspots and refugia, and the potential of populations for adaptation can be incorporated when they become available (Stelzenmüller et al., 2018).

Marine spatial planning (MSP) is advocated as a means to implement an EBM and is an iterative management process which aims to manage human activities to achieve predefined planning goals and objectives (Stelzenmüller et al., 2013). Recent evaluations of existing plans revealed that only a minority explicitly define operational objectives in relation to overarching planning goals or visions (Buhl-Mortensen et al., 2017; Collie et al., 2013). As yet, most existing plans give little attention to climate change mitigation and adaptation in their stated planning goals or objectives (Gissi et al., 2019). One exception is the Scotland national marine plan, which explicitly considers climate change both in terms of how actions under the plan might help mitigate the degree of anthropogenic-induced climate change, and how the plan needs to be adapted to account for effects of climate change (Marine Scotland, 2014). In general, a prerequisite for the implementation of a management measure should be an evaluation of the effectiveness of that measure in, for example, reducing climate change induced effects on the ecosystem state and function according to the respective management objectives (Cormier et al., 2018).

Accordingly, modifying planning objectives and management measures due to new available knowledge on conservation prioritization or the emergence of new climate change policies and regulations are part of an adaptive management process (Parma, 1998), and most MSP initiatives do allow for such future adaptations. MSP processes embedding adaptation to climate change might need to accommodate different evaluation cycles for different planning objectives, hence, acknowledging local ecosystem requirements (Sarà et al., 2018). According to good practice in EBM, an iterative evaluation process should address the (1) assessment of the potential impacts of climate change on marine habitats, species, ecosystem functions and services using sound scientific evidence and by understanding the underlying eco-evolutionary mechanisms; (2) spatial prioritization and the design of management actions to address such impacts; (3) adequate monitoring of both climatic changes and the responses of ecosystem components; and (4) the evaluation of management strategies and their modification before the cycle is repeated. The future development of decision support tools and methods that allow for instance to integrate species distribution modelling, hydrodynamic models, climate vulnerability and the adaptation potential of populations and communities (Belote et al., 2017) with assessments of cumulative pressures is essential to address climate change adaptation and mitigation in MSP processes. This strengthens the argument that future decision support tools should be much better tailored to the specific needs of marine planners and stakeholders in view of a changing world (Pınarbaşı et al., 2017).

Although insufficient ecological knowledge should not discourage climate-ready conservation action, we stress that rapid improvement in two research avenues would be incredibly helpful in our decision-making process. One is developing “early warning systems” that can then feed into flexible policy solutions each aimed at a particular scenario. The example of the Maine lobster crisis described above is one such example; for instance, having flexible quotas that respond not to last year’s stock but this year’s developing weather. The other is the identification of what factors are most likely to drive tipping points, as returning to the original state once that point is crossed can be very difficult. If we know, based on the types of information that we have explored above, that an ecosystem is approaching a tipping point, we can strive to reduce other local pressures on the system to help it cope better with the global stressors. For example, if we know that high temperature and low pH will trigger a shift, then as these signals become apparent we can implement policies to reduce stressors such as fishing pressure (Hsieh et al., 2008).

9. Conclusions

This overview highlights the required knowledge (and its current gaps) and outlines approaches and available tools for the integration of physiology, ecology and evolution in marine conservation planning. Further, it lays out the basis for how this knowledge can be used to assist in the generation of flexible conservation strategies and policy recommendations. The combination of current and historical trends, experimental studies of physiological vulnerability and altered species interactions (field and lab), -omics technologies and forecasting tools are essential for delineating the spatiotemporal heterogeneity of climate change impacts and species adaptation potential. Studying patterns of extreme events and their impacts

could help detecting approaching tipping points and facilitate exploration of micro-eco-evolutionary processes. The growing recognition that species performance and dynamics have highly mosaic patterns along their distributional range, points to the need for research focused on the seascape at multiple scales to identify potential climate hotspots and refugia. Focusing on species traits, inter- and intra-population variability in physiology, species interactions and mechanisms of local adaptation and phenotypic plasticity could also help to identify pathways for increasing resilience of sensitive ecosystem components. As climate change driven community re-structuring can gradually or abruptly (due to extreme events) alter ecosystem functioning and services, these important aspects also need to be better assessed. Finally, the mounting evidence of climate change related ecological impacts has to be effectively integrated into MSP processes by including climate change risks into cumulative effects assessments, considering climate change-related eco-evolutionary processes in conservation prioritization, and implementing adaptation and mitigation strategies within an iterative process allowing the evaluation and modification of management strategies as our knowledge base improves.

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Appendix A. Supplementary data

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